

Into the wood and back: morphological adaptations to the wood-boring parasitoid lifestyle in adult aulacid wasps (Hymenoptera: Aulacidae)

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Abstract.—A substantial sample of the parasitoid wasp family Aulacidae was examined for external morphological characters in the adults that might serve to facilitate ovipositing in and emerging from wood. The character evolution of these traits was evaluated by tracing them on a recently published phylogeny, and their functional anatomy is discussed. Various features might serve as ovipositor guides or to help remove debris during emergence from the wood, and/or to protect vulnerable body parts during emergence. It is possible to infer collaboration between different body parts to achieve the successful completion of these crucial life history stages. Variation among the taxa examined indicates that the contribution of the individual body parts to complete these tasks in some instances have changed during the evolution of the Aulacidae.

Aulacidae comprises 221 extant species belonging to two genera (Turrisi et al. 2009): *Aulacus* Jurine, 1807, with 75 species and *Pristaulacus* Kieffer, 1900 (including the former *Panaulix* Benoit, 1984), with 146 species. Both genera are represented in all zoogeographic regions, except Antarctica (Kieffer 1912; Hedicke 1939; Smith 2001, 2005a, 2005b, 2008; He et al. 2002; Jennings et al. 2004a, 2004b, 2004c; Turrisi 2004, 2005, 2006, 2007; Jennings and Austin 2006; Sun and Sheng 2007a, 2007b; Turrisi et al. 2009; Smith and Vilela de Carvalho 2010). Aulacidae have a fairly good fossil record, with 37 described species (Nel et al. 2004; Jennings and Krogmann 2009). The oldest record is from the Lower Cretaceous, but most fossil species are from the Cenozoic, with taxa recorded from the Upper Eocene of the Isle of Wight, Baltic, and Paris basin amber, and the Oligocene of North America (Nel et al. 2004).

Aulacidae are koinobiont endoparasitoids of wood-boring larvae of Hymenoptera and Coleoptera (Gauld and Hanson

1995; Jennings and Austin 2004). Hosts are larval Xiphydriidae (Hymenoptera) and, more frequently, Buprestidae and Cerambycidae (Coleoptera) (Skinner and Thompson 1960; Barriga 1990; Visitpanich 1994; Turrisi 1999, 2007; Smith 2001; Jennings and Austin 2004).

Parasitizing hosts situated deep within a tough, woody substrate requires the adult wasp to overcome certain obstacles. The challenge can be broken down into three crucial stages: 1) locating the host inside the wood; 2) ovipositing through the wood on or near the host; 3) emerging from the wood after completing the larval development. Information on the adaptations of Aulacidae are rare (Skinner and Thompson 1960; Quicke and Fitton 1995), often being part of more comprehensive studies dealing with parasitoid Hymenoptera in general (Quicke 1997; Vilhelmsen 1997a, 2003a).

The main sources for aulacid biology is Skinner and Thompson (1960), who provided detailed footage of the behaviour of

Aulacus striatus Jurine, 1807 parasitizing *Xiphydria camelus* (Linnaeus, 1758), and Deyrup (1984) in a note on *Aulacus burquei* (Provancher, 1882), a parasitoid of *Xiphydria maculata* Say, 1836. The female of *Aulacus striatus* locates the hole bored by its host, inserts the ovipositor and lays an egg in the egg of the host. When the xiphydriid larva hatches, it contains a small larva of *A. striatus*. The parasitoid larva feeds internally, delaying its development until the host larva has fed for almost a year and is close to the wood surface. Before pupating, the host larva tunnels up to the surface but not through the bark, which is left as a seal. When the host larva is about to pupate, the parasitoid rapidly completes its development, causing the death of the host. The mature parasitoid larva then emerges from the remains of the host and spins a cocoon outside the host in which it pupates. The aulacid imago emerges about two weeks later, by gnawing a hole through the bark and the thin cap of debris left by the host (Skinner and Thompson 1960; Deyrup 1984).

Concerning host location in Aulacidae, the only behavioural information was provided by Visitpanich (1994), who observed a female *Pristaulacus* sp. antennating wood containing potential host eggs and probing the eggs with the antennae as well as the ovipositor. There is no anatomical information indicating the presence of a vibration detecting system similar to the one employed for host detection by other wasps parasitizing wood-boring insects, e.g., Orussidae (Vilhelmsen et al. 2001) and Stephanidae (Vilhelmsen et al. 2008). Since at least some aulacids apparently oviposit through the borehole made by its host (see below), they may rely more on olfactory clues than on vibration detection when attempting to locate a host, as demonstrated for the parasitoid wasp family Ibaliidae (Spradbery 1970).

In this paper we investigate the external morphology of the adults of Aulacidae,

discussing possible function of different features during oviposition into and emergence from the woody substrate. We discuss the character evolution of the relevant traits in relation to the recently published phylogeny of the family by Turrisi et al. (2009).

MATERIALS AND METHODS

Taxa examined.—We examined a substantial sample of Aulacidae, containing 54 species: 8 *Aulacus* and 46 *Pristaulacus*, representing about one quarter of the described extant species of the family (Smith 2001; Turrisi et al. 2009). In addition, data on the morphology of seven fossil and about 30 more extant species were included in the discussion on the basis of descriptions and/or recent revisions. The depositories of the material examined are listed below, the acronyms are according to Evenhuis and Samuelson (2004).

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| AEIC | American Entomological Institute, Gainesville, Florida, U.S.A. (through the courtesy of Dr David R. Smith). |
| BMNH | The Natural History Museum, London, United Kingdom (Dr Stuart J. Hine). |
| BPBM | Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A. (through the courtesy of Dr David R. Smith). |
| CAS | California Academy of Sciences, San Francisco, California, U.S.A. (through the courtesy of Dr David R. Smith). |
| CNCI | Canadian National Collection of Insects and Arachnids, Ottawa, Ontario, Canada (Dr John Huber). |
| DBAC | Dipartimento di Biologia Animale "Marcello La Greca", Università di Catania, Museo Zoologico, "Turrisi G.F. Collection", Italy. |

- DEI Deutsches Entomologisches Institut, Müncheberg, Germany (Prof. Joachim Oehlke, Dr Andreas Taeger).
- HNHM Hungarian Natural History Museum, Budapest, Hungary (Dr Sandor Csoz).
- IBLP Instytut Badawczy Lesnictwa, Warszawa, Poland (Dr Jacek Hilszczański).
- ITLJ National Institute for Agro-Environmental Sciences, Insect Systematic Laboratory, Tsukuba (Ibaraki), Japan (Dr Koji Yasuda, Dr Kazuiho Konishi).
- LACM Los Angeles County Museum of Natural History, Los Angeles, California, U.S.A. (through courtesy of Dr David R. Smith).
- MCFS Museo Civico di Storia Naturale, Ferrara, Italy (Dr Fausto Pesarini).
- MCNC Museo de Ciencias Naturales, Canaria Islands: Tenerife, Spain (Dr Gloria Ortega).
- MCSN Museo Civico di Storia Naturale "G. Doria", Genova, Italy (Dr Roberto Poggi).
- MFNB Museo Friulano di Storia Naturale, Udine, Italy (Dr Carlo Morandini).
- MHNG Muséum d'Histoire Naturelle de la Ville de Genève, Switzerland (Dr Bernhard Merz).
- MNHN Muséum National d'Histoire Naturelle, Laboratoire d'Entomologie, Paris, France (Dr Claire Villemant).
- MNMS Museo Nacional de Ciencias Naturales, Madrid, Spain (Dr Carolina Martín).
- MRAC Musée Royal de l'Afrique Centrale, Tervueren, Belgium (Dr Eliane De Coninck).
- MSNP Museo Civico di Storia Naturale di Calci, Pisa, Italy (Dr Pier Luigi Scaramozzino).
- MRSN Museo Regionale di Storia Naturale, Torino, Italy (Guido Pagliano).
- MZLU Museum of Zoology, Lund University, Lund, Sweden (Dr Roy Danielsson).
- NMW Naturhistorisches Museum, Wien, Austria (Michael Madl).
- OLML Oberösterreichisches Landesmuseum, Linz, Austria (Dr Fritz Gusenleitner).
- SAMC South African Museum, Cape Town, Republic of South Africa (Ms. Margie A. Cochrane).
- USNM National Museum of Natural History, Smithsonian Institution, Washington DC, U.S.A. (Dr David R. Smith).
- ZFMK Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn, Germany (Dr Dirk Rohwedder).
- ZIN Zoological Institute of the Russian Academy of Science, St. Petersburg, Russia (Dr Sergey Belokobylskij).
- ZMHB Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (Dr Frank Koch).
- ZMUC Zoological Museum, Copenhagen University, Denmark.
- ZSMC Zoologische Staatssammlung, Munich, Germany (Prof. Dr Klaus Schönitzer, Erich Diller, Dr Stefan Schmidt).

Extant taxa directly examined.—*Aulacus bituberculatus* Cameron, 1899; *A. burquei* (Provancher, 1882); *A. digitalis* Townes, 1950; *A. impolitus* Smith, 1991; *A. pallipes* Cresson, 1879; *A. japonicus* Konishi, 1990; *A. schoenitzeri* Turrisi, 2005; *A. striatus* Jurine, 1807; *Pristaulacus africanus* (Brues, 1924); *P. barbeyi* (Ferrière, 1933); *P. bicornutus* (Schletterer, 1890); *P. boninensis* Konishi, 1989; *P. capitalis* (Schletterer, 1890); *P. chlapowskii* Kieffer, 1900; *P. compressus* (Spinola, 1808); *P. comptipennis* Enderlein, 1912; *P. editus* (Cresson, 1880); *P. edoardo*

Turrisi, 2007; *P. fasciatus* (Say, 1829); *P. fasciatipennis* Cameron, 1906; *P. flavicrurus* (Bradley, 1901); *P. foxleei* (Townes, 1950); *P. galitae* (Gribodo, 1879); *P. gibbator* (Thunberg, 1822); *P. gloriator* (Fabricius, 1804); *P. haemorrhoidalis* (Westwood, 1851); *P. insularis* Konishi, 1990; *P. intermedius* Uchida, 1932; *P. irenae* (Madl, 1990; formerly in *Panaulix*); *P. iridipennis* (Cameron, 1900); *P. kostylevi* (Alekeyev, 1986); *P. krombeini* Smith, 1997; *P. lindae* Turrisi, 2000; *P. longicornis* Kieffer, 1911; *P. minor* (Cresson, 1880); *P. montanus* (Cresson, 1879); *P. morawitzi* (Semenow, 1892); *P. mourguesi* Maneval, 1935; *P. niger* (Shuckard, 1841); *P. occidentalis* (Cresson, 1879); *P. paglianoii* Turrisi, 2007; *P. patrati* (Audinet-Serville, 1833); *P. pilatoi* Turrisi, 2006; *P. resutorivorus* (Westwood, 1851); *P. rex* (Benoit, 1984; formerly in *Panaulix*); *P. rufipilosus* Uchida, 1932; *P. rufitarsis* (Cresson, 1864); *P. ryukyensis* Konishi, 1990; *P. sexdentatus* Kieffer, 1904; *P. signatus* (Shuckard, 1841); *P. smithi* Turrisi, 2006; *P. stigmaterus* (Cresson, 1864) and *P. strangaliae* Rohwer, 1917, *P. thoracicus* (Westwood, 1841).

Fossil taxa evaluated from descriptions.—*Aulacus eocenicus* Nel, Waller, Ploëg, 2004 from the Lower Eocene of the Paris basin amber (Nel et al. 2004); *Pristaulacus bradleyi* (Brues, 1910), *P. rohweri* (Brues, 1910), and *P. secundus* (Cockerell, 1916) from the Oligocene of Florissant (Colorado, U.S.A.) (Brues 1910; Cockerell 1916); *P. praevolans* (Brues, 1923) and *P. mandibularis* Brues, 1932 from the Upper Eocene of the Baltic Amber (Brues 1923, 1932); *P. velteni* Jennings and Krogmann, 2009 from the Eocene of the Baltic Amber (Jennings and Krogmann 2009).

Methods of examination.—Observation of external features was carried out on dry preserved specimens with stereomicroscopy and SEM. Digital photographs were made using a Nikon Coolpix 4300 4.0 megapixel digital camera and enhanced using Adobe Photoshop CS® software. SEM micrographs were made using a Philips XL-20. Some pinned and air-dried

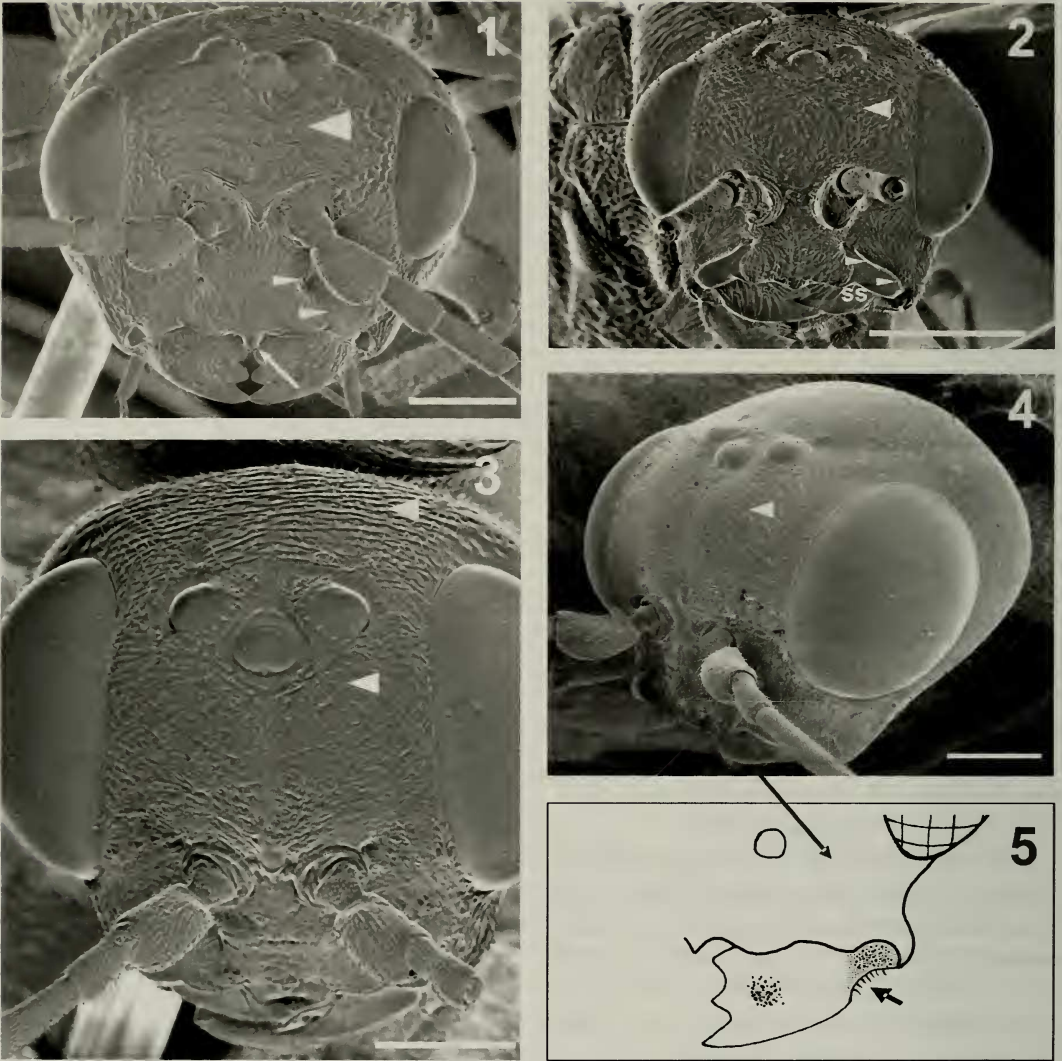
specimens were fixed with Leit-C-plast on an object table and observed at 1.6 kV using a special low voltage anode (spot size: 4–5); other specimens were coated with a Polaron SEM sputter coater system prior to observation at 10 kV using a conventional high voltage anode (spot size: 3–4).

Morphological terms.—Morphological terminology follows Crosskey (1951), Huber and Sharkey (1993) and Gauld and Bolton (1996). Terminology for surface sculpture follows Harris (1979).

RESULTS AND DISCUSSION

Morphological traits of adult aulacids directly observed or taken from literature are reviewed and briefly described in the following and illustrated prior discussing their possible functional value in relation to: 1) oviposition and 2) emergence from the wood.

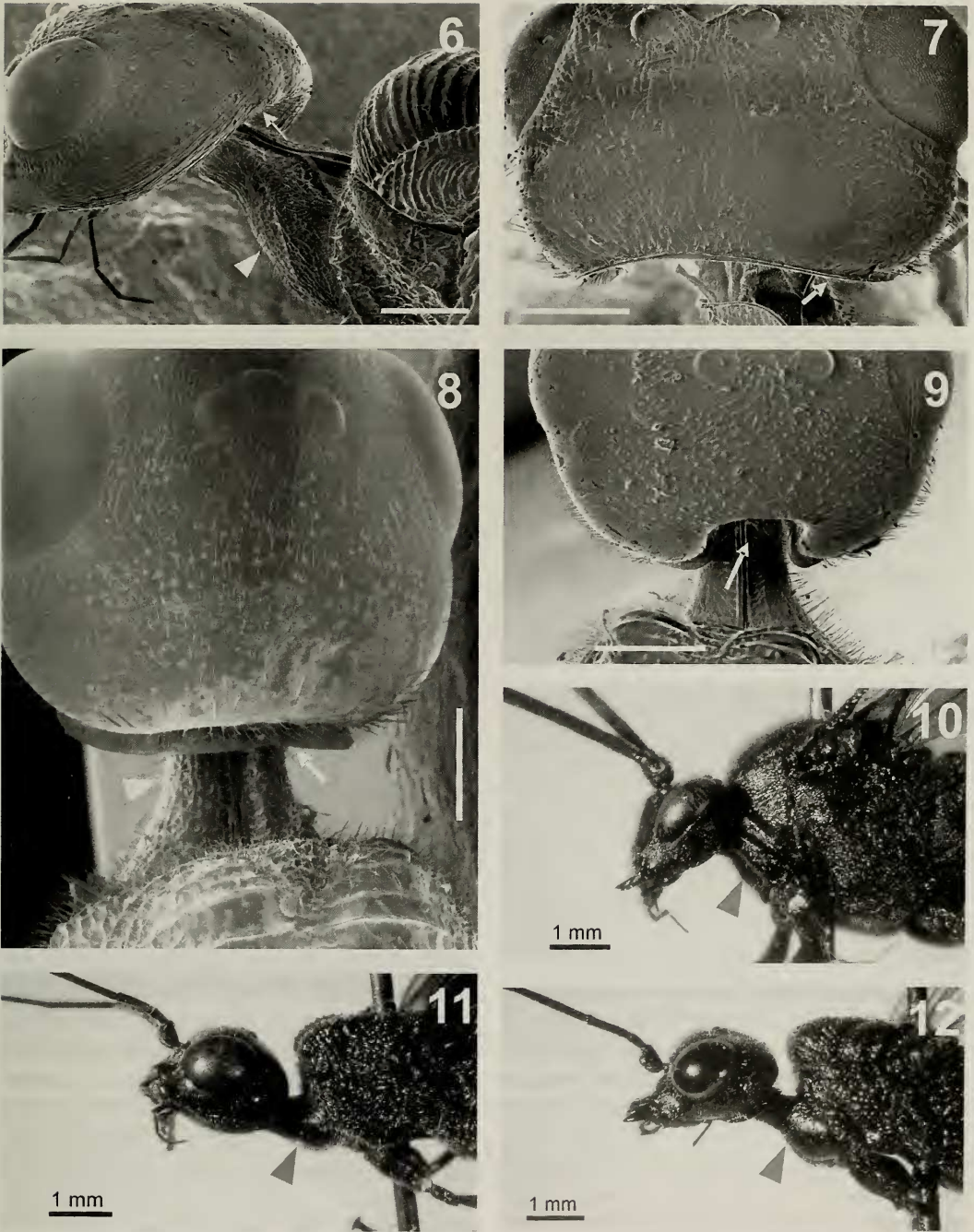
Head.—*Frons and vertex:* The frons is smooth or strongly transverse-carinulate in both fossil and extant *Aulacus* (Fig. 1). A few species of both fossil and extant *Pristaulacus* have the frons weakly transverse-rugulose or striolate-carinulate (Figs 2–3), while most species of this genus, including the fossil *P. velteni* have the frons smooth, at most punctate (Fig. 4). In *Aulacus bituberculatus* and *Pristaulacus tuberculiceps*, the vertex has two prominent posterodorsally directed outgrowths. **Subantennal grooves:** The subantennal grooves are concavities located below the toruli, accommodating the scapes when the antennae are held in a ventral position, e.g., during emergence from the pupa (Vilhelmsen 1997a). The grooves surround the tentorial pits and extend lateroventrally to the lateral areas of the clypeus. The configuration of the subantennal grooves is not known for any fossil species. They are present but not deep in all examined species of *Aulacus* (Fig. 1) and more prominent in all examined species of *Pristaulacus* (Fig. 2). **Clypeus:** All extant species of Aulacidae have a medial process on the



Figs. 1–5. Head of Aulacidae, frontal view: 1, *Aulacus striatus*; 2, *Pristaulacus gibbator*; 3, *Pristaulacus barbeyi*; 4–5, *Pristaulacus compressus*. Larger triangles indicate the sculpture of the frontal area and of the vertex, with or without transverse roughness. Smaller triangles indicate the subantennal groove. Arrow in Fig. 1 indicates the median tooth-like clypeal process. Arrow in Fig. 5 indicates the mandibular groove. Scale bars = 500 μ m.

anterior margin of clypeus, as does the extinct species *Pristaulacus mandibularis*. It is a forward protruding tooth-like process in *Aulacus* and most *Pristaulacus* (Fig. 1), while in *P. rex* it is a lamelliform process. The medial process is indistinct in the fossil *Pristaulacus velteni* (Jennings and Krogmann 2009). **Mandibles:** Both fossil and extant Aulacidae have robust mandibles, with a well developed cutting edge. Moreover, all examined species have a subbasal

transverse groove (Fig. 5) on each mandible. **Posterior margin of the head and occipital carina:** The posterior margin of the head, in dorsal view, is straight or weakly concave in all fossil and nearly all extant species (Figs 6–8). Fossil and extant species of *Aulacus* usually have no occipital carina, except for a few Australasian species where a narrow carina is present (Turrisi et al. 2009). *Aulacus* spp. may have weakly developed transverse-striolate or



Figs. 6–12. Head and anterior part of mesosoma of Aulacidae: 6, *Aulacus striatus* (lateroposterior view); 7, *Pristaulacus gibbator* (dorsal view); 8, *Pristaulacus compressus* (dorsal view); 9, *Pristaulacus comptipennis* (dorsal view). Figs 10–12. Position of the head in relation to the propleura length and to the hind margin of head, lateral view; 10, Unidentified Ichneumonidae; 11, *Pristaulacus comptipennis*; 12, *Pristaulacus compressus*. Arrows indicate the occipital area, without (Fig. 6) or with (Figs 7–8) occipital carina, or with median groove (9). Triangle in Figs 6, 8, 10–12 indicates the propleura. Scale bars = 500 μ m (Figs 6–9).

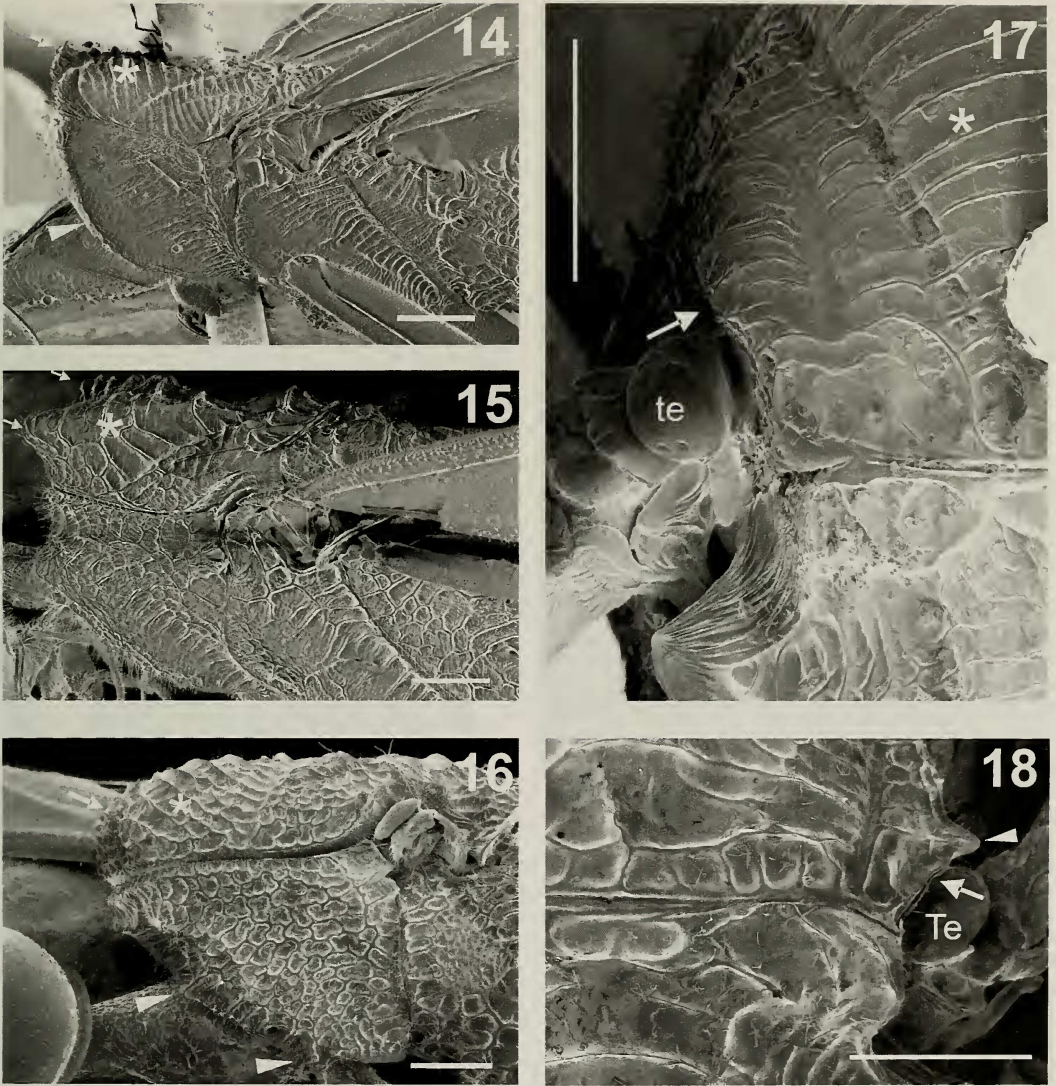


Fig. 13. Lateral view of mesosoma of *Aulacus striatus*. Arrow indicates the anterior margin of mesoscutum. Triangle indicates the lateroventral margin of pronotum. Star indicates the sculpture of mesoscutum. Scale bar = 500 μm .

rugulose sculpture (Fig. 6) on the occiput. Almost all *Pristaulacus* spp. have an occipital carina, but the occiput is smooth (Figs 7–9). In fossil *Pristaulacus* spp. the carina is very narrow; in extant species it varies from very narrow (Fig. 7) to very wide and lamelliform (Fig. 8), with a width varying from 0.2 to 1.5 \times the diameter of an ocellus. A small clade of extant *Pristaulacus* from the Oriental and Eastern Palaearctic regions, comprising *P. comptipennis*, *P. boninensis*, *P. emarginaticeps*, *P. excisus* and *P. insularis*, is characterized by a more or less wide and deep median groove interrupting the occipital carina medially (Fig. 9).

Mesosoma.—**Lateroventral margin of pronotum:** The lateroventral margin of the pronotum is rounded and without a tooth-like processes in all *Aulacus* spp., as well as in all fossil and a few extant *Pristaulacus* spp. (Figs 13–14). In the remaining species of *Pristaulacus*, it is angulated anteriorly and more or less acute; moreover, in most species, the lateroventral margin of the pronotum bears one or two anterolaterally directed tooth-like processes (Figs 15–16). **Propleura:** The propleura are elongate in all Aulacidae, forming an extended 'neck' between the head and the rest of the mesosoma (Figs 6, 8–9, 11–12). The propleura are less elongate

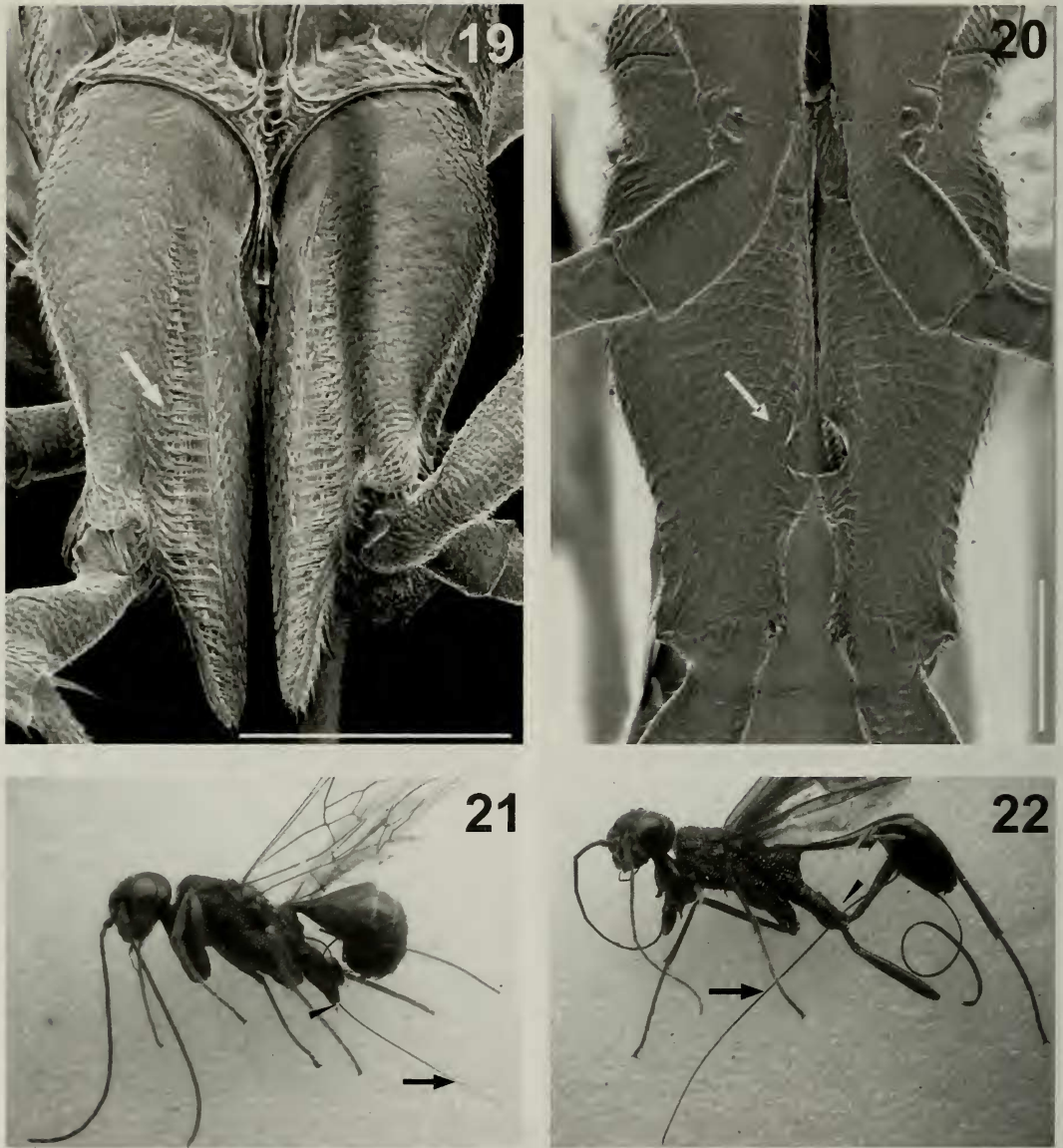
in fossil species. **Sculpture of mesoscutum:** The mesoscutum is weakly sculptured (transverse-carinate) in fossil and extant species of *Aulacus* (Figs 13, 17) and in many fossil species of *Pristaulacus*. However, other fossil species of *Pristaulacus* (e.g., *P. praevolans* and *P. secundus*) have a moderately transverse-carinate sculpture (Cockerell 1916; Brues 1923). In the extant species of *Pristaulacus*, the sculpture varies from weakly (in a few species from Nearctic and Palaearctic Regions) to strongly (in most species) transverse-carinate (Figs 15–17). **Anterior margin of mesoscutum:** In all known fossil taxa, all extant *Aulacus* spp., and most extant *Pristaulacus* spp. the anterior margin of the mesoscutum is rounded in lateral view (Figs 6, 11–13, 16). In some extant *Pristaulacus* spp. it is acute to strongly acute and protruding anteriorly, and in a few species also dorsally (Figs 14–15). **Parascutal carina:** The parascutal carina extends from the anterior part of the mesoscutum to the tegula in all Aulacidae examined. In many fossil and extant taxa the morphology of the mesoscutum is not described in detail. On the basis of a drawing from Cockerell (1916: 103, fig. 9b), the posterior part of the parascutal carina is expanded into a parascutal lobe to cover the tegula in the fossil *Pristaulacus secundus*. In the fossil *Pristaulacus velteni* the parascutal carina is expanded, with tooth-like lateral projection (Jennings and Krogmann 2009). The lobe is absent in the examined extant species of *Aulacus* and no tooth-like process is present above the tegula (Figs 17). In the examined extant species of *Pristaulacus*, the parascutal lobe is present, and most of them have a suprategular tooth-like process (Fig. 18). **Hind coxae:** The configuration of the hind coxae is not known in detail in most fossil taxa. In *Aulacus eocenicus* and a few extant *Aulacus* spp., no groove is present on the medial surface of the coxae. In all other extant species of *Aulacus* a longitudinal (Fig. 19) or (in a few Neotropical species) a transverse hind coxal groove is present.



Figs. 14–18. Mesosoma of Aulacidae: 14, *Pristaulacus kostylevi* (lateral view); 15, *Pristaulacus ryukyuensis* (laterodorsal view); 16, *Pristaulacus compressus* (lateral view); 17, *Aulacus striatus* (dorsal view); 18, *Pristaulacus compressus* (dorsal view). Arrows in Figs 14–16 indicate the anterior margin of mesoscutum. Triangles indicate the lateroventral margin of pronotum; in Fig. 14 there is no tooth-like process; in Fig. 16 two tooth-like processes are present. Arrow in Figs 17–18 indicates the posterior part of the parascutal carina; in Fig. 17 it is without a parascutal lobe and tooth-like supratergular process; in Fig. 18 the parascutal lobe and tooth-like supratergular process (triangle) are present. Star indicates the sculpture of mesoscutum. Te, tegula. Scale bars = 500 μ m.

When a longitudinal groove is present (e.g., *A. striatus*), the hind coxa also has a distal lobe (Fig. 19). A transverse hind coxal groove is present in all extant *Pristaulacus* spp. being situated either sub-apically (Fig. 20) or, very rarely, subbasally (Turrisi 2006, fig. 15) and the apical lobe is

absent. In the fossil *Pristaulacus velteni* the subapical transverse hind coxal groove is indistinct (Jennings and Krogmann 2009). **Tarsal claws:** (see Turrisi et al. 2009, fig. 11) In all *Aulacus* spp. the tarsal claws have only a very small basal tooth-like process; three tooth-like processes are present in the



Figs. 19–22. Hind coxae (ventral view), hind coxal ovipositor guide, and orientation of ovipositor during oviposition; Figs 19 and 21, *Aulacus* sp.; Figs 20 and 22, *Pristaulacus* sp. White arrow indicates the hind coxal ovipositor guide. Black arrow indicates the ovipositor. Triangle indicates the distal part of hind coxae. Scale bars = 500 μm (Fig. 19 from Jennings 2006 *in litteris*).

fossil *Pristaulacus praevolans* and *P. velteni* (Jennings and Krogmann 2009); two to six tooth-like processes (mostly four), including the basal one, in the extant species of *Pristaulacus*.

Metasoma.—**Petiole:** In Aulacidae, the petiole is inserted dorsally on the mesosoma away from the metacoxal foramina,

and it is always fused with the second segment of the metasoma, forming a rigid structure. The petiole is stocky (about as long as wide) in all fossil and most extant species of *Aulacus* (Fig. 21), as well as most fossil and a few extant species of *Pristaulacus*. In most extant *Pristaulacus* spp., the petiole is elongate and slender, between

two and five times longer than wide (Fig. 22). **Ovipositor:** In the fossil *Aulacus eocenicus*, the ovipositor is moderately long, about $0.9\times$ the fore wing length. In other fossil Aulacidae, the ovipositor is not preserved in its entirety. The length of ovipositor is highly variable within extant species. In *Aulacus* spp. it varies from 0.4 to $0.9\times$ of the fore wing length. In *Pristaulacus* spp. it varies from 0.6 to more than $2.0\times$ the fore wing length (usually more than $1.0\times$).

Adaptations for oviposition in wood.—Concerning oviposition, the main problem for hymenopteran parasitoids of xylophagous larvae is to reach the host concealed inside the wood. The tapering and elongate petiole possessed by most extant species of *Pristaulacus* (Fig. 22) together with the dorsal articulation of the petiole possibly allows a wider range of vertical movement of the metasoma with respect to the mesosoma and may improve the handling of the ovipositor. The dorsal insertion of the metasoma facilitates positioning the ovipositor vertically, thus making it possible to employ a long ovipositor (see Vilhelmsen et al. 2001). It has been suggested that the acquisition of the wasp-waist in Apocrita, through the modification of the first metasomal segment, served as a key adaptation to parasitism on hosts living inside wood (Quicke 1997; Vilhelmsen 1997b, 2000). Aulacidae and many other parasitoid wasps with long external ovipositors have transversely subdivided ovipositor sheaths which might facilitate supporting the ovipositor tip in the early stages of drilling (Vilhelmsen 2003a), although aulacids hold their ovipositor sheaths up, away from the substrate.

The cuticle of the ovipositor of Aulacidae is not impregnated with metals, in contrast to some other Hymenoptera that parasitize xylophagous insect larvae (Quicke et al. 1998). This is probably because aulacids oviposit using pre-existing crevices, e.g., the borehole made by the host female during oviposition (Skinner and Thompson 1960), thus obviating the need to

reinforce the ovipositor cuticle for drilling. Instead, the aulacid female employs an ovipositor steering device formed by blocking features at the distal ends of the ovipositor valve interlocking system (Quicke and Fitton 1995). This allows the aulacid to bend the ovipositor tip laterally, thus facilitating guiding the ovipositor through the wood. An additional ovipositor guide in Aulacidae is formed by the hind coxae (Yasumatsu 1937; Jennings and Austin 2004; Turrisi 2004). It is not known whether the species of *Aulacus* without a coxal groove use the hind coxae to guide the ovipositor. In *Aulacus* spp. with a longitudinal hind coxal groove, the coxae when aligned create a longitudinal channel in which the ovipositor is inserted (Fig. 19), guiding it backwards and slightly ventrally (Fig. 21). In all species that have a transverse hind coxal groove, the coxae (Fig. 20), when aligned form a transverse channel guiding the ovipositor anteroventrally (Fig. 22) at an angle depending on the relative positions of the coxae and the metasoma. The internal diameter of this channel is a little wider than the ovipositor, allowing for small movements of the latter and the opportunity for fine steering.

According to Turrisi et al. (2009) the transverse hind coxal groove was acquired very early in the evolution of Aulacidae, even if it is not a ground plan character for the family, and it is retained by most aulacids. A longitudinal hind coxal groove was acquired twice independently within *Aulacus* in a Holarctic clade and by two Australasian species (Turrisi et al. 2009). The shift in orientation of the hind coxal grooves from transverse to longitudinal implies a change in ovipositor mechanism. There seems to be no clear correlation of groove orientation with any of the other features observed (e.g., ovipositor length), and it is at present unclear to us what advantages this reorientation of the ovipositor direction may confer.

The two basalmost extant species of *Aulacus* (*A. wau* and *Aulacus* 'sp. 1') as well

as some fossil taxa (Nel et al. 2004) do not have a hind coxal guide, apparently the plesiomorphic condition within the family. However, Townes (1950) suggested that the absence of the hind coxal grooves may be secondary; this seems to be the case for the small clade *Aulacus brevicaudis* + *A. impolitus* (Turrisi et al. 2009). According to Townes (1950), the absence of the coxal groove was caused by shortening of the ovipositor obviating the need for a structure to guide it. Indeed, both *Aulacus brevicaudis* and *A. impolitus* have comparatively short ovipositors. However, in the fossil *Aulacus eocenicus*, the ovipositor is moderately long, about $0.9\times$ fore wing length, although no hind coxal ovipositor guide is present (Nel et al. 2004).

Adaptations for emerging from wood.— Many structures of parasitoid wasps pupating within wood are possibly emergence-facilitating adaptations, for example to break down and remove the debris plug sealing the pupal chamber, while other structures assure protection of delicate structures such as antennae and wings. To remove the debris plug, aulacids use mainly their mandibles (Skinner and Thompson 1960; Quicke et al. 1998), but the head capsule and mesosoma also participate. The role of the head in making progress through the gallery within the wood is evident from Skinner and Thompson (1960). The wasp moves the head up and down, and also laterally, to cut and remove the debris. The median clypeal process (Figs 1–5) may facilitate crumbling of the plug and penetration of the head into the massive plug. A structure with a similar function is present in other parasitoid wasps (e.g., Stephanidae and some Ichneumonidae) pupating within wood (Quicke 1997).

The outgrowths from the vertex in *Aulacus bituberculatus* and *Pristaulacus tuberculiceps* (clearly an evolutionary convergence) perhaps have a similar function to the ocellar corona (a circlet of cuticular projections around the median ocellus)

observed in Orussidae (Vilhelmsen 2003b) and Stephanidae (van Achterberg 2002), although in the latter two families the projections are in a slightly more anterior position. The ocellar corona has been suggested to be used to brace the head of the wasp while chewing an escape tunnel or help the wasp drag itself along its gallery (Engel and Grimaldi 2004).

A well developed transverse striolate-carinulate sculpture is present on the frons of fossil taxa of both *Aulacus* and *Pristaulacus*, and it is present in several extant species of *Aulacus* (Fig. 1). It is reasonable to assume that this sculpture plays an important role during emergence of the imago of these taxa, since the massive debris plug needs to be reached and cut by the mandibles, and then pushed away (Skinner and Thompson 1960). In other extant *Aulacus* spp. and in most extant *Pristaulacus* spp., the sculpture of the frons is weak or even absent (Figs 2–4), but a more or less developed transverse-carinate sculpture is always present on the mesosoma. Based upon inference from the phylogeny of Turrisi et al. (2009), the sculpture on head and mesosoma arose simultaneously within Aulacidae, suggesting a close functional linkage of these tagmata to help adult emergence from the wood early in the evolutionary history of the family. This is the case of most extant "*Aulacus*" spp. and many fossil aulacids, in which the important role of the head during emergence from wood might have been further facilitated by the presence of an angulated anterior head margin. In contrast, head sculpture is secondarily reduced or lost and the anterior margin of the head is rounded in most extant *Pristaulacus* spp. as well as in a few lineages of extant "*Aulacus*" spp., whereas the mesosomal sculpture remained and still could assume an important role in removal of debris within the wood gallery.

It seems that in the more ancestral species of Aulacidae (i.e., the "*Aulacus*" grade) the head plus the mesosoma share

the tasks of crumbling and removing the debris plug, whereas in more derived aulacids (extant *Pristaulacus* spp.) the head has mainly the task of penetrating, crumbling and cutting the debris. The function of removing the debris is mainly undertaken by the mesosoma. In addition, the mesosoma might serve to brace the body during emergence, leaving the head free to break down the frass plug; the absence of distinct sculpture on the head might make it less prone to get stuck when executing this task. The acute shape of the anterior margin of mesoscutum and the marginal horn-like processes on the pronotum in many extant species of *Pristaulacus* may be interpreted as adaptations to these functions, and thus facilitating the emergence of the imago from the wood gallery (Figs 14–16).

The 'neck' formed by the elongate propleura, a feature shared by all extant Aulacidae (Figs 11–12) as well as the Gasteruptiidae (Turrisi et al. 2009), might also help removing debris. Elongate propleura allow wider movements of the head in the vertical plane and makes it possible to employ the mandibles forward in a prognathous position (Fig. 12; see also below). The occipital carina in *Pristaulacus* spp. possibly serves to protect the occipital area, especially around the foramen magnum, from incursion of debris. The enlargement of the occipital carina, forming an extended lamina dorsal to the neck (Fig. 8) in most extant *Pristaulacus*, would enhance this function. The development of this protective structure is probably correlated with the length of the propleura that increases the distance between head and mesosoma, and exposes the occipital area to penetration by debris. In addition, the enlarged occipital carina might help displacing debris during emergence. The presence of a broad occipital carina might restrict the dorsal tilting of the head due to interference with the propleura (Figs 8, 12). A medial groove is situated on the hind margin of the head in a subclade of

Pristaulacus. The width of the groove is evidently correlated with the width of the propleura (Fig. 9), fitting around them; this enables wider dorsal movement of the head and consequently the mandibles can be employed in a prognathous position (Fig. 11), even more so than in taxa without the medial groove (Fig. 12). The groove allows the wasp to lock its head against the propleura: this might facilitate gaining purchase for the mandibles and pushing away debris with the head.

In some endoxylic parasitoid wasps (e.g., Ibalidae, Stephanidae), cuticular horn-like processes of the body, mainly on the mesosoma, are believed to be adaptations to emerging from hard substrates and for protecting delicate parts of the body (Quicke 1997; Vilhelmsen 1997a). Likewise, it is possible that the presence of one or two tooth-like processes on the lateroventral margin of pronotum in many species of *Pristaulacus* may help pushing the imago along when it ecloses from the wood.

The legs obviously play an important role when the adult wasp moves through the galleries in the wood and emerges from it. According to Turrisi et al. (2009), the presence of a simple claw is a plesiomorphic feature of Aulacidae, and the pectinate claw is an autapomorphy of *Pristaulacus*. In conjunction with this, the increased number of tooth-like processes on the tarsal claws (Turrisi et al. 2009), may be interpreted as another emergence-facilitating adaptation, enhancing the insect hooking against the walls of the tunnel when it pushes forward. Given that the claws are in constant contact with the substrate also after emergence, they might have other functions as well.

During emergence, the antennae and wings of the adult wasp are highly susceptible to damage. The extant species of *Aulacus* have weakly developed subantennal grooves (Fig. 1), while in many extant *Pristaulacus* spp., they are more developed (Fig. 2). The presence of subantennal and mandibular grooves, and the

tendency of the former to become deeper in more derived species (*Pristaulacus* spp.) may be interpreted as adaptations to protect the antennae. During emergence the subantennal and mandibular grooves accommodate the bases of the antenna, whose remaining part is curved poster-oventrally (see also Vilhelmsen 1997a), thus reducing the risk of damage.

The point of articulation of the fore wing is also vulnerable during emergence from the wood. In taxa where a parascutal lobe and sometimes a suprategular tooth-like process are present (e.g., *Pristaulacus* spp.), they probably serve to protect the wing base (Fig. 18) from abrasion against the gallery sides, as opposed to *Aulacus* spp. where these features are absent (Fig. 17).

CONCLUDING REMARKS

In this paper we have argued that many morphological features of the aulacid imago may be interpreted as adaptations to the lifestyle as parasitoid of wood-boring insects. In particular, they might facilitate oviposition into the wood and emergence out of it. The species of *Pristaulacus* appear to be more specialized due to the presence of several morphological features (occipital carina, parascutal lobes and suprategular spines, pectinate tarsal claws) not shared by *Aulacus* spp.

Some adaptations occur in other families of Hymenoptera with a similar life style, including the hind coxal ovipositor guide (Turrisi et al. 2009), found in some Braconidae (Cenocoeliinae) and Ichneumonidae (Labeninae) (Townes 1950; Turrisi 2004), obviously instances of convergence, and the ovipositor steering mechanism (Quicke and Fitton 1995).

In Aulacidae, it is possible to infer cooperation between structures on different body parts (e.g., the median process on the clypeus, the head and mesosoma sculpture, and perhaps the pectinate tarsal claws) during emergence from the wood. Furthermore, the character combinations displayed by different taxa indicate shifts in emphasis of the function of different

body parts (e.g., both head and mesosomal sculpture in *Aulacus* spp. to predominantly mesosomal sculpture in *Pristaulacus* spp. during emergence).

In the present paper we have aimed to show that it is possible to correlate detailed morphology with the intricacies of lifestyle in parasitoid Hymenoptera. We hope that it will inspire further studies that will elucidate this diverse and biologically important life style, both within Aulacidae and in other parasitoid wasps.

ACKNOWLEDGMENTS

We are grateful to Prof. Dr Klaus Schönitzer (Zoologische Staatssammlung, Munich, Germany) for making comments on an early draft of the manuscript and Dr John Jennings (School of Earth and Environmental Sciences, University of Adelaide, Australia) who made substantial comments on a later version of the manuscript. We are also grateful to Prof. Giovanni Pilato and Prof. Giorgio Sabella (University of Catania) for useful comments and suggestions on an early draft of the manuscript. Thanks also to: Prof. Dr Matthias Starck (Zoological Institute of the Ludwig-Maximilians-Universität, Munich, Germany) for allowing us to make the SEM micrographs, and Prof. Dr Klaus Schönitzer for his technical assistance. We are indebted to the curators of the numerous museums and to the colleagues (see "Materials and Methods") who provided material for this study. This research was financially supported by the University of Catania, Fondo Ricerca d'Ateneo (ex 60%).

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